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SPECIES-BUILDING BY HYBRIDIZATION AND MUTATION

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THE mystery that has surrounded the origin of new species in the incipient stages of their evolution has lately been penetrated and cleared away to a large extent by the light of studies in Mendelian inheritance and the attendant idea of mutation. Species building is no longer a hypothetical process based on the preservation of minute, useful, fortuitous variations, but it is a process open to observation and experimental control. Its raw materials are variations that are usually not minute, useful or fortuitous, but clean-cut unit characters, tending to vary only in certain limited, well-defined directions depending upon the chemical peculiarities and physical structure of the particular form of protoplasm, and, in the vast plurality of cases, nonuseful.

The fields of systematic zoology and botany, illuminated by the new science, genetics, are emerging from the mists of formalism, and invite biologists of the broadest type to exploration. The geneticist turns to systematics for many of the materials with which to solve the problems of organic evolution. The systematist sees that in order to keep abreast of the times he must stand ready to rebuild his pigeonholes and test with experiment that which he puts into them.

Every one occupied with zoology or botany realizes that there are no adequate criteria by which this or that assemblage of individuals is or is not to be regarded as a

distinct species. Arbitrary rules for species making, designed to restrict the activities of the more vigorous "splitters" have been indeed laid down by experienced and conservative systematists. The final test, however, so far as any exists, is acknowledged to be whether a group breeds approximately true to its kind and is approximately sterile with other closely related stock, and yet in how few cases have both or either of these criteria been actually applied by the describer of species!

As a matter of fact no stock that has been bred on a vast scale, so far as I am aware, breeds absolutely true to specific characters. In Morgan's *Drosophila*¹ and De Vries's *Oenothera*, numerous mutants appear, probably through the absence of certain chemical elements, or by unusual combinations of elements, in the chromatin of the germ plasm. That this phenomenon has not been shown for many other species is due, in all probability, to lack of close attention to all the individuals in a huge procession of stock in the process of breeding. Any insect bred as extensively as *Drosophila ampelophila*, the pomace fly, has been would probably show as many mutants; some would show more. *Colias eurytheme*, the "orange sulphur" or alfalfa butterfly, is such an example. Though this butterfly can not be bred on a scale comparable with *Drosophila*, every thousand individuals yield many discontinuous variations: red eyes instead of green, tongue uncoiled instead of wound in close flat spiral when at rest, one antenna shorter than the other, the absence of certain spots from the wings, gynandromorphism, caterpillars with two longitudinal rows of large black dorso-lateral spots or white dorso-lateral stripes upon a dorsal surface usually unmarked, caterpillars with one proleg less upon one side than the other. This is a partial list of points at which the descendants of three females of *Colias eurytheme* failed in a single summer to breed true to the characteristics of the species, though bred under uniform normal conditions. The fact that these discontinuous

¹ *Science*, N. S., Vol. XXXIII, Nos. 847, 849, pp. 496-499, 534-537, 1911.

variations appear under uniform external conditions leads one to be very skeptical toward most of the past experimental work supposed to show the effects of the environment upon insects in modifying the germ cells. Any one wishing to try an experiment on the production of variations by the influence of the environment, or upon the inheritance of acquired characteristics, should deny himself absolutely this privilege until he shall have bred under normal conditions at least a thousand individuals of the stock that he will subsequently employ.

That species necessarily breed true to the specific characters ascribed to them by their inventors is an unverified dogma. At best the reporter picks out stray individuals here and there from a vast procession of which he can only see glimpses, and, trusting to the credulity of the public in the established ideas about these matters, he creates upon paper a new species. Doubtless the unit characters of "specific" grade in the stock of some species are more generally constant or homozygous than those of certain others, but it is reasonable to suppose that, owing to dominance the heterozygous² condition regarding certain characters is frequently masked and unnoticed in apparently pure strains of wild stock. If the heterozygote respecting a certain character be comparatively rare, or if it be a heterozygote based on several interacting factors, like redness in the kernel of Nilsson-Ehle's wheat,³ it may cross again and again with the homozygous dominant, or with another heterozygote of similar nature to itself, without the appearance in the population of the recessive. That specific and varietal characters do exist in heterozygous condition in wild stock of "pure" species, unmasked by dominance and easily detected, I have found to be the case in *Colias* at several points. The color pattern as a whole apparently fluctuates in variation, but these variations in detail are

² The mixed Mendelian condition, $D(R)$, producing germ cells D and R in equal numbers.

³ *Act. Univers. Lund*, 190

strictly a matter of inheritance. Its "fluctuation" is not due to a difference in environmental conditions surrounding different individuals, but evidently to the condition of the germ plasm. The parents of any brood may be heterozygous or homozygous for the determiners of color pattern. If they come from a strain homozygous in this respect and are alike in appearance, the offspring will resemble the parents closely and show a narrow range of variation, but if unlike and derived each from unlike parents, a wide range of inherited "fluctuation" occurs. Such is often the case in the inheritance of a melanic tendency so often attributed to the action of the environment, and of spots used in the diagnosis of species as, for example, the conspicuous spot in the middle of the under side of the hind wing. This is commonly double in *Colias philodice* and *C. eurytheme*, consisting of a chief and an accessory spot, single in *C. palæno*, an arctic circumpolar species, but it varies enormously. In *eurytheme* and *philodice* the accessory spot may be absent; in *palæno*, in rare cases, it may be present. I have bred large families of *C. eurytheme* in which both the chief and accessory spots were, like those of the parents, almost uniformly large and nearly equal in size. In other families, from parents in which the accessory spot is nearly or quite lacking, the offspring show a similar reduction. In *C. philodice* I have found it possible by selection to establish a race devoid of the row of submarginal red-brown spots of the under side of the wings. Thus, by selection, strains, nearly or perhaps quite homozygous for definite points of color pattern, may be established, derived from a population which in the main is in an extremely heterozygous condition. Yet species are named and distinguished on the basis of these features.

Another example of heterozygous condition of a character within a wild species is the white pigment in the ground color of the "albino" female of *Colias*, both in the yellow species, *philodice* and the orange species, *eurytheme*. The white female is regularly heterozygous

for this sex-limited character. Her daughters are white or colored (yellow or orange, as the case may be) in equal numbers. Still another interesting heterozygous feature, though not of "specific" grade, was seen last summer in a pure strain of *Colias eurytheme*. A female appeared that could not upon stimulation coil up her tongue. Mated with a normal male, this abnormality was inherited in various degrees by half her offspring (37 uncoiled and 28 coiled). One of her daughters, abnormal in this respect and mated with a normal of a different strain, transmitted the abnormality to about 16 per cent. of her offspring (29:151), showing that the possessor of this abnormality is regularly heterozygous in respect to it.

Whether *Ænothera lamarckiana* is or is not a complex hybrid produced from two American species, is it not certain that, like other wild and cultivated stock, it does possess characters for which it is heterozygous, and that the watcher for mutants frequently seizes upon rare combinations of recessive features as a part of his elementary species?

But to breed true is only a secondary criterion of species. Inbred strains of domestic animals and plants do that to a certain degree. Varieties and races to a certain extent may do the same. The real criterion (and the one least often practically used by the systematist) is fertility within the group and sterility with other closely related groups. Here dogma holds sway among writers on organic evolution as well as among systematists, for we are told by those who have been accustomed since childhood to the idea of the objective reality of species that hybridization of species, that is, genuine species in good and regular standing before the scientific public, has played very little part in the origin of new species. This attitude was entirely logical in view of the accepted ultimate definition of a species. If the individuals of one species are actually sterile with members of another, hybridiza-

tion of species can not play an important part in the manufacture of new wild strains. But only in comparatively rare instances have attempts been made experimentally to mate Linnaean species. The dogma of the objective reality and uniform value of the species unit has diverted us from seriously attacking this problem. Just as in the nineteenth century the fixed idea of the immutability of species blocked the progress of the doctrine of evolution, so this dogma now stands in our way, and obstructs the possibility of vision. We need now fully to recognize the fact, which most biologists are ready to admit, that the term species is applied to most heterogeneous groups of individuals, groups of every conceivable size, based on differences that are most diverse in number and importance, often separated from allied groups entirely by the arbitrary judgment of the describer, and depending ultimately upon his personal temperament. These groups, as already stated, have been tested in comparatively few instances by the only reputable criterion that can be applied in the separation of closely allied groups, that of sterility or fertility *inter se*.

To one who tries to divest himself of the accepted ideas regarding species and is on the watch for evidence of hybridization among unlike strains that we are accustomed to call species, new cases of such hybridization frequently come to light. Especially is this true among the insects. In regions where the faunal areas of two "good" species overlap or are contiguous, such crossing not infrequently occurs.

A most interesting case is that of the four species of the coccinellid beetle *Adalia* that occur in the same region in Colorado, as worked out by Palmer.⁴ These four forms with clean-cut differences in color and color pattern had been named and described by different authors as distinct species, yet three of them were found to be interbreeding with complete fertility but still respectively maintaining their identity, forming a regular Mendelian

⁴ *Annals Entom. Soc. America*, IV, 3, September, 1911.

epistatic series: a red-brown spotless form, *melanopleura*, dominant at one end of the series, then *annectans*, a red-brown, spotted type, and finally the recessive, melanic, red-spotted *humeralis* with a color pattern different from that of *annectans* or of *Coloradensis*, another red-brown, spotted type of that locality. "But" says the upholder of the present idea of species, "here we have a single polymorphic species, not three or four different species. The breeding experiments show that the describers of these forms were wrong in ascribing systematic rank to mere color varieties." It goes, of course, almost without saying that the makers of these species did not before naming their beetles, breed them to determine whether they would breed true to type and were infertile *inter se*. Indeed, in how few cases has this been done! Even the larval stages of most known beetles are imperfectly unknown, much less the possible genetic relationship of one type to another, as determined by breeding them to maturity. Blaisdell⁵ describes the case of two Californian Coccinellidæ which are found in winter in small groups under the bark of eucalyptus trees. "Usually there was one *Olla plagiata* with each of the groups [of *O. abdominalis*], irrespective of whether they were made up of two or more individuals." The same author, by selection of specimens of *abdominalis* representing different types of color pattern, describes its range of variation, but adds that his studies throw no light on the relationship of the two species. Had he bred certain individuals of *O. abdominalis* together, it is not at all unlikely, in view of his observation of the regular occurrence of a few *plagiata* in every group of *abdominalis*, that the former interbreeds with the latter and may be a simple recessive in respect to it. Miss Palmer's work on the allied *Adalia* certainly suggests this as a possibility.

Another remarkable case is that of the nine true-breeding species of grouse-locust, *Paratettix*, recently de-

⁵ *Entom. News*, Vol. 24, No. 9, November, 1913.

scribed by Nabours.⁶ These nine color types, or species, freely interbreed. The color pattern of the resulting F_1 hybrid in each case is a mosaic combination of those of the two parents. The latter in subsequent inbreeding may be extracted intact, each having been transmitted as a distinct unit, without dominance.

In Lepidoptera, an order in which polymorphism is notoriously common, hybridization between species has been frequently observed. Standfuss⁷ devotes eight octavo pages of his excellent "Handbuch" simply to the enumeration of examples of such hybridization between palæarctic species of moths and butterflies, and acknowledges that he mentions only a fragment of all such cases on record or preserved in collections. This list would be greatly extended if American species were included. Seven different hybrid combinations within the genus *Colias* in the palæarctic region have been noted by Standfuss.

Colias philodice, the clouded sulphur or clover butterfly of the eastern and central United States, readily crosses with *C. eurytheme*, the orange sulphur or alfalfa butterfly of the western and central states. The territory of *philodice*, according to Scudder extends like a wedge westward from the Atlantic into the faunal area of *eurytheme*. Overlapping thus occurs in the Mississippi Valley, though *philodice* does not extend as far southward as the Gulf States, Texas, Louisiana and Mississippi, in which *eurytheme* is found.

These two species are fairly sharply distinguished by the difference in the ground color, which in *eurytheme* is orange, in *philodice* sulphur yellow. The middle spot of the upper side of the hind wing is brilliant orange in *eurytheme*, pale orange or yellow in *philodice*. The dark border of the hind wing of the female is wider in *eurytheme* than in *philodice* and broken with a row of large yellow spots.

⁶ *Journal of Genetics*, Vol. 3, No. 3, February, 1914.

⁷ "Handbuch d. paläarktischen Gross-Schmetterlinge," 1896, p. 51-53.

It has long been known that these two species hybridize in the Mississippi Valley, where both occur. By extended experiments during the past summer and previous autumn with *eurytheme* stock sent to me from Arizona through the kindness of Messrs. V. L. Wildermuth and R. N. Wilson and with *philodice* from New Hampshire, I have found that the two species mate together readily, and produce vigorous offspring. The species-hybrid males were then mated with *eurytheme* females, and more than half of the pairs (viz., four out of seven) were fertile. Mated together, however, the species-hybrids showed much sterility. Out of ten such matings, nine were infertile. From the tenth pair, nineteen adult butterflies were produced.

Orange in this cross is distinctly dominant over no orange, or yellow, but the color of the heterozygote is a pale orange overlying yellow, and is by no means as brilliant as the almost fiery orange of the large, summer seasonal variety, the typical "*eurytheme*." In broods emerging the last week in August and the first three weeks of September, when intense color may be expected, the heterozygote is pale orange, corresponding approximately to the variety known as *keewadin*, whereas those raised in the greenhouse and emerging early in December, resemble the small orange-yellow winter type known as *ariadne*. *Keewaydin*, according to Wright,^s occurs at all seasons in California, though probably more abundantly in spring and autumn. Hence he regards this as the typical variety, rather than "*eurytheme*." It is intermediate, however, in size and intensity of color.

In general, therefore, there is an incomplete dominance of orange, the color of the heterozygote corresponding either to that of the intermediate or to that of the winter, seasonal variety of *eurytheme*, depending upon the time of the year when, and the environmental condition under which, the cross is made. The wide, spotted margin of the hind wing in the female *eurytheme*, moreover, when pres-

^s "Butterflies of the West Coast of the United States," p. 119.

ent in marked degree, is dominant over the narrower margin in *philodice*. This dominance of the orange manifests itself quite as distinctly if the albino female of *eurytheme*, instead of the orange female, is bred to the yellow *philodice* male. The daughters of such a family in one case (0, 1913) were 36 white, 35 orange; the sons, numbering 72, were, of course, all orange. The white species-hybrid (F_1) is identical in appearance with the albino *eurytheme*, the female color pattern of the latter (wide marginal bands) being dominant, and the orange middle spot both in pure bred albino *eurytheme* and in the albino hybrid being usually paler than in their orange sisters.

The second hybrid generation inbred (F_2) shows a well marked segregation of the sulphur-yellow color of *philodice*, as a simple Mendelian recessive. Three out of the sixteen colored (non-albino) individuals of the brood obtained in December, 1913, are definite recessives of clear sulphur yellow, with pale yellow middle spots on the hind wing. The most highly colored individuals are four that correspond in hue to pale examples of the light orange-yellow winter variety, *ariadne*. There is no return, at least in this winter brood (enclosed in a greenhouse in New Hampshire in December), to the brilliant orange of the grandparental *eurytheme* stock. Nor do they even return to the suffused light orange (intermediate) tint of the heterozygous father (*keewadin* type), for the ground color of all individuals of this brood (F_2) is *yellow*, either flushed or spotted, except in three individuals, with orange.

An interesting case of probable hybridization in the allied genus *Meganostoma*, or dog's head butterfly, is recorded by Wright⁹ between the Californian *M. eurydice* and *M. casonia*, common throughout the southern states. The two species are remarkably different in color and have different food plants. The male of *eurydice* differs from that of *casonia* in having a violet luster and lacking

⁹ *Loc. cit.*, p. 116.

the black border upon the hind wings possessed by *cæsonia*; in the female, *eurydice* is clear yellow with no dark border, while in *cæsonia* the female has a wide border similar to that of its male, though less well marked on the hind wings. The probable hybrid called *amorphæ* is a female, intermediate in color between the typical *cæsonia* and *eurydice*. That is, the border of *cæsonia* crossed with no border (if my interpretation is correct) is incompletely dominant. Wright says:

At one time I was of the opinion that *Amorphæ* was a hybrid between *Eurytheme* and *Caesonia* . . . but of late years, as no male *Amorphæ* is known, I have concluded that *Amorphæ* is simply a dimorphic female [of *eurydice*].

Possibly it is both, an example of dimorphism produced either by immediate hybridization, or by a mutation resulting from some previous hybridization. That a male appears to be lacking in this case would not be an argument against the possibility of hybridization, for by such crossing the sex ratio is frequently upset, the product being of one sex only. But it appears to be possible that the male of this cross is that described as *M. bernardino*, a variety of *eurydice* found in the mountains of the same region where *amorphæ* also occurs. It is an interesting combination of the male coloration of both species, having the violet hue of *eurydice* that is lacking in *cæsonia* and having the dark border of the hind wings of *cæsonia* lacking in *eurydice*. Its female is described as being smaller than that of *eurydice*, but otherwise practically identical with it. This case, as Wright has suggested, is a most inviting subject for further study, and, judging by what he says of the sexual instincts of the *eurydice* male—"a wooer . . . energetic and persistent, not hesitating to ignore all rules of propriety, of species and of genera"—not difficult of experimental management.

The genus *Basilarchia*, the admiral butterflies, is well known for the hybridization of its very unlike species, *B. arthemis* the "banded purple" of the northern states,

B. astyanax the "red-spotted purple" of the southeastern states. The hybrid species, *B. proserpina*, occurs in a zone in which their two faunal areas overlap. In this same group is the common "viceroy" *B. archippus*, the range of which roughly covers that of both the other species and extends further westward, touching the Pacific coast in Washington (Scudder). The experiments of Edwards, and especially of Field, have shown that these three well-differentiated pure species occupying contiguous, or in respect to *archippus* overlapping, territory are in some cases at least mutually fertile. *B. arthemis* and *astyanax* regularly interbreed in the narrow zone where *proserpina* occurs. *Proserpina*, the hybrid, usually shows the general dominance of the *astyanax* characters (lack of white band).

From eggs laid by a wild female *proserpina* Edwards¹⁰ secured three *arthemis*, one *proserpina*. Field¹¹ raised from a similar lot of eggs nine *proserpina*, seven *arthemis*. Presumably in each case the male parent was the recessive *arthemis*, and hence equal numbers of the two types would be expected. Field has also succeeded in crossing a ♀ *astyanax* with a ♂ *arthemis*, and a ♀ viceroy, *archippus*, with a ♂ *arthemis*, the latter pair producing nine males intermediate in color. Specimens of an apparent hybrid, intermediate in color between *astyanax* and *archippus*, have also occasionally been captured.

The complete overlapping of the faunal area of *archippus* upon those of the two other species indicates that, though crossing sometimes occurs, the resulting hybrids are probably usually sterile, though this matter has not yet been thoroughly investigated. *Proserpina*, however, is a fertile and extraordinarily variable hybrid. In view of its great variability it appears, by the way, not impossible that *archippus*, the red-brown "mimic" of the monarch, *Anosia plexippus*, may have arisen as a mutation from the hybrid *proserpina*, though the wide-spread

¹⁰ *Canadian Entomologist*, Vol. IX, 1877.

¹¹ *Psyche*, Vol. XVII, No. 3, 1910.

range of *archippus* at present and our ignorance of the state of the *Basilarchia* stock at the time of the origin of the "mimic" make any such specific historical guess hazardous. It may, however, some time be possible by experimental breeding to extract from this red-spotted purple hybrid a red-brown type similar to *archippus*. If the *Basilarchia* stock were as easily bred as *Drosophila*, one might be very confident of accomplishing this. In any event, the theory of the origin of mimicry by natural selection is, in the opinion of the writer, entirely superfluous, though this celebrated monarch-vice-roy case should be exhaustively studied by experimental methods, to determine whether natural selection now operates in any degree in the matter.

Examples of clusters of interbreeding types may be drawn in large numbers from various classes of animals and plants. Bateson¹² has recently called attention to the interesting case of the two American flickers described by Allen,¹³ the eastern *Colaptes auratus* and the western and Mexican *C. cafer*, which hybridize in the zone in which their faunal areas overlap, the American grackles, the golden-winged and blue-winged warblers and their hybrids, Lawrence's and Brewster's warblers, and others.

In reference to the common purple grackle, which Chapman¹⁴ regards as a hybrid between the Florida grackle and the bronzed grackle, Ridgeway¹⁵ says:

My own opinion in the matter exactly coincides with Mr. Chapman's but since so many forms now ranked as sub-species are similarly involved I prefer, at present, to leave the matter in abeyance.

This significant statement from a master of ornithological taxonomy indicates that hybridization among American birds is a promising subject for investigation.

Of the *occasional* mutual fertility of unlike strains different enough to be classed as unquestionable species,

¹² "Problems of Genetics," 1913, Chap. VII.

¹³ *Bull. American Mus. Nat. Hist.*, Vol. IV, 1892.

¹⁴ *Ibid.*

¹⁵ "Birds of North and Middle America," Part 2, p. 219, 1902.

there also can be no doubt. "We can only escape the conclusion that some species are fully fertile when crossed," wrote Darwin,¹⁶ "by determining to designate as varieties all the forms that are quite fertile," and he added that some plants exposed to unnatural conditions are so modified "that they are much more fertile when crossed by a distinct species than when fertilized by their own pollen."

The rareness of these crosses between unlike strains or species and the partial sterility of the offspring are not obstacles in the way of regarding occasional hybridization as one of the chief sources of mutation and hence eventually of new species, for, as my preliminary experiments in hybridizing species of *Colias* have already shown, there may exist within a strain of species-hybrids certain individuals that are fertile, though the most of their brothers and sisters, mated, respectively, in a similar way, are sterile. Nature probably makes more random experiments in hybridization than we imagine; many fail; some succeed; and in especially favorable stock like *Colias*, judging from the numbers of closely allied but different types (species) occurring in the same localities in western Asia or in northwestern United States and British America, probably many succeed.

In seeking to determine how mutation, whether the result of hybridization or of possible climatic influences, acts in the production of new species, it is possible from cases already at hand to suggest possible steps in the evolution of distinct, mutually infertile, types from one comparatively simple polymorphic species.

The well-known dimorphic European currant moth, *Abraxas grossulariata*, in which the light-colored (recessive) variety, *lacticolor*, is found in nature only in the female sex, will serve as an example of an elementary condition. *Lacticolor* males, as Doncaster¹⁷ has shown,

¹⁶ "Animals and Plants under Domestication," Vol. II, Chap. 19, p. 179.

¹⁷ "Report of the Evolution Committee," 4, 1908.

may readily be bred. When one of these males is mated with a *lacticolor* female, there is produced in captivity a pure *lacticolor* strain. If *lacticolor* males and females should be segregated and allowed to breed together until they have become as abundant as the typical form, this case would then resemble that of the Colorado lady beetles of the genus *Adalia*, described above, in that it would consist of different types maintaining their identity while freely interbreeding with complete fertility. The *Abraxas* complex differs from the *Adalia* species-cluster, however, in the occurrence of sex-linkage in the inheritance of the *lacticolor* variety, whereas in *Adalia* the factors for the different color patterns apparently are distributed in the gametogenesis of a heterozygous individual without sex-linkage, freely and at random.

A more advanced stage in evolution is that represented by the *Basilarchia* species-cluster, in which partial sterility between the viceroy and the two purple species, over the faunal areas of which its own overlaps, and the difference in geographical distribution between the banded purple and red-spotted purple, keep the three elements apart.

By easy stages we may in imagination pass on to groups composed of closely allied species which sterility and local segregation completely separate from one another; groups that probably have arisen from a polymorphic species that has broken up into its constituent parts, and thus given rise to new elementary species.

The dimorphism of *Colias* differs from that of *Abraxas* in that the color of the rarer type of female can not be transferred in the ordinary course of breeding, without further mutation, to the male. It is a sex-limited character, like the female color pattern in *Colias*, (*i. e.*, a wide dark border broken with spots) and not sex-linked like the variety *lacticolor* of *Abraxas*.

The white female of *Colias* is regularly heterozygous for color. She produces as many white daughters as

yellow, or orange, as the case may be. Evidently, in order to extract a pure white race from *C. philodice* or *C. eurytheme*, it will be necessary by a mutation to obtain first a homozygous white female, and then by a further mutation a homozygous white male. White males are known in nature as rare aberrations, but, whether they are homozygous or heterozygous for color, it is impossible to say. Among the two thousand offspring of heterozygous white females of *philodice* and *eurytheme* that I have bred since 1908, there has been not a single white male. The sons of a white female, though some are capable of transmitting the white, are always yellow or orange. I have lately, however, raised a large brood in which all the females were white. This was a "back cross" between a white female of the orange *eurytheme* and a male species-hybrid (son of a white mother). Precisely similar matings, however, gave both white and colored female offspring in equal numbers; hence in the production of this brood there was probably a mutation. From such stock as this the extraction of a pure white race from *Colias* at some time may possibly be accomplished.

In this connection it is interesting to note that we have the testimony of a good observer, the late Mr. W. G. Wright,¹⁷ who made the study of Californian butterflies his life work, to the effect that the white variety of *Colias eurytheme* "is now quite common, though twenty-five years ago it was a great rarity, and it was accounted a feat to secure one of them, and if the present rate of increase of the blond form shall go on, in a few hundred years the normal orange-colored female will be extinct and unknown." If this is a fact, and not an illusion due to a general increase in the population of *eurytheme* owing to an increase in the cultivation of the food plant, alfalfa, in that region, it may be the result of possible mutations, whereby homozygous white females may have been introduced into the population. It will be of inter-

¹⁷ *Loc. cit.*, p. 117.

est to determine whether such true-breeding white females actually occur in California.

Evolution in *Colias* is usually regarded, on the other hand, as tending towards suppression of the white stock rather than its further extension, inasmuch as *Pieris* and other allied genera are white. It seems to be a reasonable hypothesis that, by progressive mutations in *Colias* affecting first the male then the female,¹⁸ white has become yellow; yellow, orange; orange, red, or a fiery orange;¹⁹ or yellow may be transmuted into black, as in an aberration of the male in *C. philodice*. By retrogressive or degressive mutations, accordingly, we may hope to isolate from *C. philodice* or *C. eurytheme* a pure white race.

SUMMARY AND CONCLUSIONS

The erroneous idea that Linnæan species are homogeneous, well-defined groups of equal importance has done much to retard progress in the experimental study of evolution. The limits of a species are often arbitrary, depending ultimately upon the temperament of the describer, and frequently based upon ignorance of the nearest allies of the individuals described, living in other parts of the world.

The most definite criteria of species, viz., that "specific" characters are constant, and that hybrids of Linnæan species are infertile *inter se*, are only approximately correct. Characteristics of species sometimes occur in heterozygous condition. Hybrids of Linnæan species, as has long been known, are often fertile. These matters, owing to traditional, unwarranted respect for described species, have received comparatively little investigation.

Examples of hybridization in *Adalia*, *Colias*, *Meganostoma*, *Basilarchia* and *Paratettix* among insects, in *Colaptes*, *Quiscalus*, and *Helminthophila* among birds are cited.

¹⁸ In *C. dimera* of South America, for example, the female is yellow, but in the male the *fore wings* are orange.

¹⁹ As in the Asiatic *eogene*.

Occasional fertile crossing of unlike strains that rarely interbreed is a probable source of mutations and new types.

A suggestion is made that a comparatively simple polymorphic species (like *Abraxas grossulariata*) may break up into a cluster of mutually fertile elementary species (e. g., *Adalia* in Colorado). Further differentiation, involving partial sterility, may be illustrated by the *Basilarchia* species-cluster. This may be followed by the establishment, and isolation through complete sterility, of distinct types, or species in the strict sense of the term.

Evolution of color in the yellow and orange butterflies of the genus *Colias* involves white, which exists to-day in heterozygous condition in certain females. If the ancestors of *Colias* were white, as in Pierids generally, we have only to imagine a mutation in the male-producing germ cells of the original white females, by virtue of which white pigment was replaced by, or transmuted into, yellow. This would make all the males yellow, leaving all the females white, which is true of certain arctic species to-day.

A similar mutation affecting the germ cells of these white females, but introducing the factor for yellow into only half of them, would produce the heterozygous condition found in *C. philodice* and *C. eurytheme*. Pure yellow strains may readily be bred from such mixed stock, and hence, probably, it has come about that four fifths or nine tenths of the females of *C. philodice* in eastern United States are pure yellow.

Progressive mutations from yellow to orange and fiery orange, affecting first the male, then the female, have probably occurred in *Colias* in many part of the world, especially in warmer climates. Climatic conditions determine the amount of orange pigment in the cross between the orange *eurytheme* and the yellow *philodice*. This hybrid is larger and contains more orange when raised in summer than when bred in late fall and winter. *C. philodice* in this cross is a Mendelian recessive.